Title: Tree height and hydraulic traits shape growth responses across droughts in a temperate broadleaf forest

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Summary

- As climate change is driving increased drought frequency and severity in many forested regions around the world, mechanistic understanding of the factors conferring drought resistance in trees is increasingly important. The dendrochronological record provides a window through which we can understand how tree size and species' traits shape tree growth responses during droughts.

- We analyzed tree-ring records for twelve species that comprise 97% of the woody productivity of the 25.6-ha ForestGEO plot in a broadleaf deciduous forest of northern Virginia (USA) to test hypotheses on how tree height, microenvironment characteristics, and species' traits shaped drought responses across the three strongest regional droughts over a 60-year period (1950 - 2009).

- Individual-level drought resistance decreased with tree height and was not significantly linked to canopy position. The potentially greater rooting volume of larger trees did not confer an advantage in sites with low topgraphic wetness index. Resistance was greater among species whose leaves experienced less shrinkage upon desiccation and lost turgor (wilted) at more negative water potentials.

- We conclude that tree height and hydraulic traits influence growth responses during drought, as recorded in the tree-ring record spanning historical droughts. Thus, these factors can be useful for predicting future drought responses under climate change.

Key words: annual growth; canopy position; drought; Forest Global Earth Observatory (ForestGEO); leaf hydraulic traits; temperate broadleaf deciduous forest; tree height; tree-ring

Introduction

Forests play a critical global role in climate regulation (Bonan, 2008), yet there remains enormous uncertainty as to how the terrestrial carbon sink, which is dominated by forests, will respond to climate change (Friedlingstein et al., 2006). An important aspect of this uncertainty lies with physiological responses of trees to drought (Kennedy et al., 2019). In many forested regions around the world, the risk of severe drought is increasing (Trenberth et al., 2014; Dai et al., 2018), often despite increasing precipitation (Intergovernmental Panel on Climate Change, 2015; Cook et al., 2015). Droughts, intensified by climate change, have been affecting forests worldwide and are expected to continue as one of the most important drivers of forest change in the future (Allen et al., 2010, 2015). Understanding forest responses to drought requires elucidation of how tree size, microenvironment, and species' traits jointly influence individual-level drought resistance, and the extent to which their influence is consistent across droughts. However, it has proven difficult to resolve the many factors affecting tree growth during drought with available forest census data, which only rarely captures extreme drought, and with tree-ring records, which capture multiple droughts but rarely consider the roles of tree size and microenvironment.

Many studies have shown that within species, large trees tend to be more affected by drought. Greater growth reductions for larger trees was first shown on a global scale by Bennett et al. (2015), and subsequent studies have reinforced this finding (*e.g.*, Stovall et al. (2019); Hacket-Pain et al. (2016)). It has yet to be resolved which of several potential underlying mechanisms most strongly shape size trends in drought response. First, tree height may be a primary driver. Taller trees face the biophysical challenge of lifting water greater distances against the effects of gravity and friction (McDowell et al., 2011; McDowell and Allen, 2015; Ryan et al., 2006; Couvreur et al., 2018). Vertical gradients in stem and leaf traits–including smaller and thicker leaves (higher leaf mass per area, LMA), greater resistance to hydraulic dysfunction (*i.e.*, more negative water potential at 50% loss of hydraulic conductivity, more negative P50), and lower hydraulic conductivity at greater heights (Couvreur et al., 2018; Koike et al., 2001; McDowell et al., 2011)–enable trees to become tall (Couvreur et al., 2018). Indeed, tall trees require xylem of greater hydraulic efficiency, such that xylem conduit diameters are wider in the basal portions of taller trees, both within and across species (Olson et al., 2018; Liu et al., 2019), and throughout the conductive systems of angiosperms (*Zak et al. 2010, Olson et al. 2014,2018*). Wider xylem conduits plausibly make large trees more vulnerable to embolism during drought (Olson et al., 2018), and traits conducive to efficient water transport may also lead to poor ability to recover from or re-route water around embolisms (Roskilly et al., 2019). Second, larger trees may have lower drought resistance because they tend to occupy more exposed canopy positions, where they experience higher solar radiation, greater wind speeds, and lower relative humidity (**REFS–KAT**). Subcanopy trees tend to fare better specifically due to the benefits of a buffered environment (Pretzsch et al., 2018). Third, large trees tend to have larger root systems, which potentially counteracts some of the biophysical challenges they face by allowing greater access to water; however, it appears that this effect is usually insufficient to offset the costs of height and/or crown exposure. Finally, tree size-related responses to drought can be modified by species' traits and their distribution across size classes (Meakem et al., 2018; Liu et al., 2019). Understanding the mechanisms driving the greater relative growth reductions of larger trees during drought will require sorting out the interactive effects of height, canopy position, root water access, and species' traits.

Debates have also arisen regarding the traits influencing tree growth responses to drought. *It has been observed that ring-porous species showing higher drought tolerance than diffuse-porous species (Friedrichs*

et al., 2009; Elliott et al., 2015; Kannenberg et al., 2019), but this classification does not resolve differences among the many species within each category. Commonly-measured traits including wood density and leaf mass per area (LMA) have been linked to drought responses in some temperate deciduous forests (Abrams, 1990; Guerfel et al., 2009; Hoffmann et al., 2011; Martin-Benito and Pederson, 2015) and other forest biomes around the world (Greenwood et al., 2017). However, in other cases these traits could not explain drought tolerance (Maréchaux et al., 2019), or the direction of response was not always consistent. For instance, higher wood density has been associated with greater drought resistance at a global scale (Greenwood et al., 2017), but it correlated negatively with tree performance during drought in a broadleaf deciduous forest in the southeastern United States (Hoffmann et al., 2011). Thus, the perceived influence of these traits on drought resistance may actually reflect indirect correlations with other traits that more directly drive drought responses (Hoffmann et al., 2011). Recent work has shown a great potential for hydraulic traits to predict growth and mortality responses. Hydraulic traits including water potentials at which percent loss of conductivity surpass a certain threshold ($P50$, $P80$, $P88$) and hydraulic safety margin correlate with drought performance (Anderegg et al., 2018) but are time-consuming to measure and therefore infeasible for predicting or modeling drought responses in highly diverse forests (*e.g.*, in the tropics). More easily measurable leaf hydraulic traits with direct linkage to plant hydraulic function can explain greater variation in plant distribution and function (Medeiros et al., 2019). These include leaf area shrinkage upon desiccation (PLA_{dry}) (Scoffoni et al., 2014) and the leaf water potential at turgor loss point (π_{tlp}), *i.e.,* the water potential at which leaf wilting occurs (Bartlett et al., 2016). The abilities of both PLA_{dry} and π_{tlp} to explain tree performance under drought remains untested.

Here, we examine how tree height, microenvironment characteristics, and species' traits collectively shape drought responses. We test a series of hypotheses and associated specific predictions (Table 1) based on the combination of tree-ring records from three droughts (1966, 1977, 1999), species functional and hydraulic trait measurements, and census data from a large forest dynamics plot in Virginia, USA. First, we focus on the role of tree height and its interaction with microenvironment. We test hypotheses designed to disentangle the relative importance of tree height; crown exposure; and soil water availability, which should be greater for larger trees in dry but not in perpetually wet microsites. Second, we focus on the role of species' functional and hydraulic traits, testing the hypothesis that species' traits--particularly leaf hydraulic traits--predict Rt. We test predictions that drought resistance is higher in ring-porous than semi-ring and diffuse-porous species, that it is correlated with wood density–either postively (Greenwood et al., 2017) or negatively (Hoffmann et al., 2011)– and positively correlated with LMA, and that hydraulic leaf traits including PLA_{dry} and π_{tlp} are better predictors.

Materials and Methods

Study site

Research was conducted at the 25.6-ha ForestGEO (Forest Global Earth Observatory) study plot at the Smithsonian Conservation Biology Institute (SCBI) in Virginia, USA (38°53'36.6"N, 78°08'43.4"W) (Bourg et al., 2013; Anderson-Teixeira et al., 2015a). SCBI is located in the central Appalachian Mountains near the northern boundary of Shenandoah National Park. Elevations range from 273 to 338 m above sea level with a topographic relief of 65m (Bourg et al., 2013). Climate is humid temperate, with mean annual temperature of 12.7°C and precipitation of 1005 mm during our study period (1960-2009; source: CRU TS v.4.01; Harris et al. (2014)). Dominant tree taxa within this secondary forest include *Liriodendron tulipifera*, oaks (*Quercus*

123 spp.), and hickories (*Carya* spp.).

124 *Data collection and preparation*

125 Within or just outside the ForestGEO plot, we collected data on a suite of variables including tree size,
126 microenvironment characteristics, and species traits (Table 2). The SCBI ForestGEO plot was censused in
127 2008, 2013, and 2018 following standard ForestGEO protocols, whereby all free-standing woody stems ≥ 1cm
128 diameter at breast height (DBH) were mapped, tagged, measured at DBH, and identified to species (Condit,
129 1998). From this census data, we used measurements of DBH from 2008 to calculate historical DBH and data
130 for all stems ≥ 10cm to analyze functional trait composition relative to tree height (all analyses described
131 below). Census data are available through the ForestGEO data portal (www.forestgeo.si.edu).

132 We analyzed tree-ring data (xylem growth increment) from 571 trees representing the twelve species with the
133 greatest contributions to woody aboveground net primary productivity ($ANPP_{stem}$), which together
134 comprised 97% of study plot $ANPP_{stem}$ between 2008 and 2013 (Helcoski et al., 2019) (Fig. **S1**). Cores (one
135 per tree) were collected within the ForestGEO plot at breast height (1.3m) in 2010-2011 or 2016-2017. In
136 2010-2011, cores were collected from randomly selected live trees of each species that had at least 30
137 individuals ≥ 10 cm DBH (Bourg et al., 2013). In 2016-2017, cores were collected from all trees found dead
138 during annual mortality censuses (Gonzalez-Akre et al., 2016). Cores were sanded, measured, and crossdated
139 using standard procedures, as detailed in (Helcoski et al., 2019). The resulting chronologies were published in
140 Zenodo (DOI: 10.5281/zenodo.2649302) in association with Helcoski et al. (2019).

141 For each cored tree, we combined tree-ring records and allometric equations of bark thickness to reconstruct
142 DBH for the years 1950-2009. Prior DBH was estimated using the following equation:

$$DBH_Y = DBH_{2008} - 2 * \left[\sum_{year=Y}^{2008} (r_{ring,Y}) - r_{bark,Y} + r_{bark,2008} \right]$$

143 Here, Y denotes the year of interest, r_{ring} denotes ring width derived from cores, and r_{bark} denotes bark
144 thickness. Bark thickness was estimated from species-specific allometries based on the bark thickness data
145 from the site (Anderson-Teixeira et al., 2015b). Specifically, we used linear regression on log-transformed
146 data to relate r_{bark} to diameter inside bark from 2008 data (Table S1), which were then used to determine
147 r_{bark} in the DBH reconstruction.

148 Tree heights (H) were measured by several researchers for a variety of purposes between 2012 to 2019
149 (n=1,518 trees). Measurement methods included direct measurements using a collapsible measurement rod
150 on small trees (NEON, 2018) or a tape measure on recently fallen trees (this study); geometric calculations
151 using clinometer and tape measure (Stovall et al., 2018a) or digital rangefinders (Anderson-Teixeira et al.,
152 2015b; NEON, 2018); and ground-based LiDAR (Stovall et al., 2018b). Rangefinders used either the tangent
153 method (Impulse 200LR, TruPulse 360R) or the sine method (Nikon ForestryPro) for calculating heights.
154 Both methods are associated with some error (Larjavaara and Muller-Landau, 2013), but in this instance
155 there was no clear advantage of one or the other. Measurements from the National Ecological Observatory
156 Network (NEON) were collected near the ForestGEO plot following standard NEON protocol, whereby
157 vegetation of short stature was measured with a collapsible measurement rod, and taller trees with a
158 rangefinder (NEON, 2018). Species-specific height allometries were developed (Table S2) using logarithmic
159 regression ($ln[H] \sim ln[DBH]$). For species with insufficient height data to create reliable species-specific

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allometries (n=2, JUNI and FRAM), heights were calculated from an equation developed by combining the height measurements across all species. We then used these allometries to estimate H for each drought year, Y, based on reconstructed DBH_Y.

Crown position–a categorical variable including dominant, co-dominant, intermediate, and suppressed–was recorded for all cored trees that remained standing during the growing season of 2018 following the protocol of Jennings et al. (1999). While some tree crowns undoubtedly changed position over the past several decades, in this case the bias would be unlikely to result in false acceptance of the prediction that dominant trees have the lowest Rt (*i.e.*, type I error unlikely, type II error possible), making our hypothesis test conservative. An analysis of crown position relative to height (Fig. **2d**) and height changes since the beginning of the study period indicated that changes between focal drought years (1966, 1977, and 1999; see below) were fairly small relative to differences among canopy positions (Fig. **S3**), with average tree height growth confined to ~0.82 m from 1966 to 1977, ~1.45 m from 1977 to 1999, and ~1.97 m from 1999 to 2018. However, dominant and co-dominant trees were similar in height (Figs. **2d**, **S3**).

Topographic wetness index (TWI) was calculated using the dynatopmodel package in R (Fig. **S1**) (**?**). Originally developed by Beven and Kirkby (1979), TWI was part of a hydrological run-off model and has since been used for a number of purposes in hydrology and ecology (Sørensen et al., 2006). TWI calculation depends on an input of a digital elevation model (DEM; ~3.7 m resolution from the elevatr package (**?**)), and from this yields a quantitative assessment defined by how "wet" an area is, based on areas where run-off is more likely. From our observations in the plot, TWI performed better at categorizing wet areas than the Euclidean distance from the stream.

Hydraulic traits were collected in August 2018 (Table 3). We sampled small sun-exposed branches up to eight meters above ground from three individuals of each species in and around the ForestGEO plot. Sampled branches were re-cut under water at least two nodes above the original cut and re-hydrated overnight in covered buckets under opaque plastic bags before measurements were taken. Rehydrated leaves taken towards the apical end of the branch (n=3 per individual: small, medium, and large) were scanned, weighed, dried at 60° C for $\geq$ 48 hours, and then re-scanned and weighed. Leaf area was calculated from scanned images using the LeafArea R package (Katabuchi, 2019). LMA was calculated as the ratio of leaf dry mass to fresh area. PLA_{dry} was calculated as the percent loss of area between fresh and dry leaves. Wood density was calculated for ~1cm diameter stem samples (bark and pith removed) as the ratio of dry weight to fresh volume, which was estimated using Archimedes' displacement. We used the rapid determination method of Bartlett et al. (2012) to estimate osmotic potential at turgor loss point (π_{tlp}). Briefly, two 4 mm diameter leaf discs were cut from each leaf, tightly wrapped in foil, submerged in liquid nitrogen, perforated 10-15 times with a dissection needle, and then measured using a vapour pressure osmometer (VAPRO 5520, Wescor, Logan, UT, USA). Osmotic potential (π_{osm}) given by the osmometer was used to estimate (π_{tlp}) using the equation $\pi_{tlp} = 0.832\pi_{osm}^{-0.631}$ (Bartlett et al., 2012).

To characterize how environmental conditions vary with height, data were obtained from the NEON tower located <1km from the study area via the neonUtilities package (**?**). We used wind speed, relative humidity, and air temperature data, all measured over a vertical profile spanning heights from 7.2 m to above the top of the tree canopy (31.0 or 51.8m, depending on censor), for the years 2016-2018 (NEON, 2018). After filtering for missing and outlier values, we determined the daily minima and maxima, which we then aggregated at the monthly scale.

Identifying drought years

We identified the three largest droughts within the time period 1950-2009, defining drought (Slette et al., 2019) as events with both anomalously dry peak growing season climatic conditions. Specifically, we used the metric of Palmer Drought Severity Index (PDSI) during May-August (MJJA; Table S3), which were identified by Helcoski et al. (2019) as the months of the current year to which annual tree growth was most sensitive at this site. PDSI divisional data for Northern Virginia were obtained from NOAA (https://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp) in December 2017. Based on this, we identified three drought years - 1966, 1977, and 1999 (Figs. **1**, **S2**, Table S3).

The droughts differed in intensity and antecedent moisture conditions (Fig. **S2**, Table S3). The 1966 drought was preceded by two years of moderate drought during the growing season and severe to extreme drought starting the previous fall and in August reached the lowest growing season $PDSI$ (-4.82) of the three droughts. The 1977 drought was the least intense throughout the growing season, and it was preceded by 2.5 years of near-normal conditions, making it the mildest of the three droughts. The 1999 drought was preceded by wetter than average conditions until the previous June, but reached the lowest PDSI during May-July (-4.53).

Statistical Analysis

For each drought year, we calculated drought resistance (Rt) as the ratio of basal area increment (BAI) during drought to the mean BAI over the five years preceding the drought (Lloret et al., 2011). Thus, Rt values <1 and >1 indicate growth reductions and increases, respectively. Because the Rt metric could be biased by directional pre-drought growth trends, we also tried an intervention time series analysis (ARIMA, (**?**)) that predicted mean drought-year growth based on trends over the past **10** years and used this value in place of the five-year mean in calculations of resistance (Rt_{ARIMA}= observed BAI/ predicted BAI). Because Rt tended to produce more reasonable estimates than Rt_{ARIMA} when there was a large difference between these metrics, we selected Rt as our focal metric, presenting parallel results for Rt_{ARIMA} in the Supplementary Info. We focus exclusively on drought resistance (Rt or Rt_{ARIMA}), and not on the resilience metrics described in Lloret et al. (2011), because (1) we would expect resilience to be controlled by a different set of mechanisms, and (2) the findings of *DeSoto et al. (2020)* suggest that Rt is a more important drought response metric for angiosperms.

Analyses focused on testing the predictions presented in Table 1, with Rt (or Rt_{ARIMA}) as the response variable. Models were run for all drought years combined and for each drought year individually. The general statistical model for hypothesis testing was a generalized linear mixed model (GLMM), implemented in the **XX** package in R [**REF**], with Rt (or Rt_{ARIMA}) as the response variable, tree nested within species as a random effect, and independent variables including drought year (multi-drought model only), $ln[H]*TWI$, crown position, and 1-2 species traits (see below). We used AICc to assess model selection, and conditional/marginal R-squared to assess model fit as implemented in the AICcmodavg package in R (**?**). AICc refers to a corrected version of AICc, and is best suited for small data sizes (see Brewer et al., 2016).

To avoid over-fitting models with five species traits (Table 2) across only 12 species, we did not include all traits as fixed effects in a single GLMM, but rather conducted individual tests of each species trait to determine the relative importance and appropriateness for inclusion in the main model. These tests followed the model structure specified above. Trait variables were considered appropriate for inclusion in the main model if they had a consistent direction of response across all droughts and if their addition to a

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²⁴² corresponding null model lacking the trait improved fit (at ΔAICc $\geq$ 1.0) in at least one drought year (Table
²⁴³ 4). We note that the ΔAICc $\geq$ 1.0 criterion is not a test of significance, but of whether the variable has
²⁴⁴ enough influence to be considered as a *candidate* variable in full models.

²⁴⁵ We then determined the best full models for predicting Rt (or Rt_{ARIMA}). To do so, we compared models
²⁴⁶ with all possible combinations of candidate variables and identified the full set of models within ΔAICc=2 of
²⁴⁷ the very top model (that with lowest AICc). When a variable appeared in all of these models and the sign of
²⁴⁸ the coefficient was consistent across models, we viewed this as support for the acceptance/rejection of the
²⁴⁹ associated prediction (Table 1). If the variable appeared in some but not all of these models, and its sign we
²⁵⁰ was consistent across models, we considered this partial support/rejection. In presentation of the results
²⁵¹ below, we note instances where the Rt_{ARIMA} model disagreed with the Rt model, but otherwise do not
²⁵² discuss the Rt_{ARIMA} model.

²⁵³ All analysis beyond basic data collection was performed using R version 3.5.3 (R Core Team, 2020). Other
²⁵⁴ R-packages aside from those already listed were very helpful in conducting analyses. These are listed in the
²⁵⁵ Supplementary Information. All data, code, and results are available through the SCBI-ForestGEO
²⁵⁶ organization on GitHub (https://github.com/SCBI-ForestGEO: SCBI-ForestGEO-Data and
²⁵⁷ McGregor_climate-sensitivity-variation repositories), with static versions corresponding to data and analyses
²⁵⁸ presented here archived in Zenodo (DOIs: 10.5281/zenodo.3604993 and [TBD], respectively.

²⁵⁹ **Results**

²⁶⁰ *Community-level and species' drought responses*

²⁶¹ At the community level, cored trees showed substantial growth reductions in all three droughts, with a mean
²⁶² Rt of 0.86 in 1966 and 1999, and 0.84 in 1977 (Fig. **1b**). Across the entire study period (1950-2009), the
²⁶³ focal drought years were the three years with the largest fraction of trees exhibiting $Rt \leq 0.7$. Specifically, in
²⁶⁴ each drought, roughly 30% of the cored trees had growth reductions of $\geq$ 30% ($Rt \leq 0.7$): 29% in 1966, 32%
²⁶⁵ in 1977, and 27% in 1999. However, some individuals exhibited increased growth, *i.e.*, $Rt > 1.0$: 26% of trees
²⁶⁶ in 1966, 22% in 1977, and 26% in 1999.

²⁶⁷ Responses varied across species and by drought (Fig. 2). Averaged across all droughts, Rt was lowest in
²⁶⁸ *Liriodendron tulipifera* (mean $Rt = \mathbf{0.66}$) and highest in *Fagus grandifolia* (mean $Rt = \mathbf{0.99}$).

²⁶⁹ *Tree size, microenvironment, and drought resistance*

²⁷⁰ Taller trees showed stronger growth reductions during drought when evaluating the three drought years
²⁷¹ together and for 1966 individually (Table 1; Fig. 4;). Specifically, $ln[H]$ appeared, with negative coefficient,
²⁷² in the top models and all models within ΔAICc=2 of these (Tables S6-S7). For the 1977 and 1999 droughts,
²⁷³ $ln[H]$ did not appear in the top models, but was included, with negative coefficient, in some of the models
²⁷⁴ that were statistically indistinguishable (ΔAICc<2) from the top model (Tables 1, S6-S7).

²⁷⁵ Crown position varied as expected with height (dominant > co-dominant > intermediate > suppressed), but
²⁷⁶ with substantial variation (Fig. **3d**). Crown position was never statistically significant (Table 1). It did,
²⁷⁷ however, come out in the top models for 1977 and 1999 (Fig. 4), and was included in some of the models
²⁷⁸ within ΔAICc=2 of the top model for 1966 and all droughts combined (Table S6). When Rt_{ARIMA} was used
²⁷⁹ as the predictor variable, crown position was never in a top model, and was included among the models
²⁸⁰ within ΔAICc=2 of the top model only for 1977. Canopy position did not have a consistent influence, when

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281 included in models within ΔAICc=2 of the top model, across years: dominant trees had the lowest Rt (or

282 Rt_{ARIMA}) in 1977, but in all other years suppressed trees had the lowest Rt (Fig. 4; Tables S6-S7).

283 In the years for which we have vertical profiles in climate data (2016-2018), taller trees–or those in dominant

284 crown positions– were generally exposed to higher evaporative demand during the peak growing season

285 months (May-August; Fig. **3**). Specifically, maximum daily wind speeds were significantly higher above the

286 top of the canopy (40-50m) than within and below (10-30m) (Fig. **3a**). Relative humidity was also somewhat

287 lower during June-August, ranging from ~50-80% above the canopy and ~60-90% in the understory (Fig. **3b**).

288 Air temperature did not vary across the vertical profile (Fig. **3c**).

289 Rt had a signficantly negative response to $ln[TWI]$ in all drought years combined and in 1977, and a

290 negative effect of $ln[TWI]$ was included in models within ΔAICc=2 of the top model in 1999 and the

291 Rt_{ARIMA} model for 1966 (Fig. 4, Tables 4-5). This negates the idea that trees in moist microsites would be

292 less affected by drought. Nevertheless, we tested for a negative $ln[H] * ln[TWI]$ interaction, which could

293 indicate that smaller trees (with smaller rooting volume) are more susceptible to drought in drier

294 microenvironments with a deeper water table. This hypothesis was rejected, as the $ln[H] * ln[TWI]$

295 interaction was never the significant, and had a positive sign in any models within ΔAICc=2 of the top

296 model in which it appeared (Tables 1, S6-S7). This term did appear, with positive coefficient, in the top

297 Rt_{ARIMA} model for all years combined (Table S7).

Species' traits and drought resistance

299 Wood density, LMA, and xylem porosity were all poor predictors of Rt (Tables 1,S4-S5). Wood density and

300 LMA were never significantly associated with Rt in the single-variable tests and were therefore excluded

301 from the full models. Xylem porosity was also excluded from the full models, as it had no significant

302 influence for all droughts combined and had contrasting effects in the individual droughts: whereas

303 ring-porous species had higher Rt than diffuse- and semi-ring- porous species in the 1966 and 1999 droughts,

304 they had lower Rt in 1977 (Table S4). It is noteworthy that the two diffuse-porous species in our study,

305 *Liriodendron tulipifera* and *Fagus grandifolia*, were at opposite ends of the Rt spectrum (Fig. 2), further

306 refuting the idea that xylem porosity is a useful predictor of Rt.

307 In contrast, PLA_{dry}, and π_{tlp} were linked to drought responses (Fig. 4; Tables 1,S4-S7). Both had consistent

308 signs across all droughts and explained modest amounts of variation (ΔAICc > 1.0) during at least one of

309 the three droughts (Table S4), qualifying them as candidate variables for the full model. PLA_{dry} had a

310 significant influence, with negative coefficient, in full models for the three droughts combined and for the 1966

311 drought individually (Fig. 4; Tables S6-S7). For 1977 and 1999, it was included, with negative coefficient, in

312 some of the models within ΔAICc=2 of the top model (Tables S6-S7). π_{tlp} was included, with negative

313 coefficient, in the top full model for all droughts combined and for the 1977 drought individually (Fig. 4;

314 Table 5). It was included in some of the models within ΔAICc=2 of the top model in 1999 (Tables S6-S7).

Discussion

316 Tree height, microenvironment, and hydraulic traits shaped tree growth responses across three droughts at

317 our study site (Table 1, Fig. 4). The greater susceptibility of larger trees to drought, similar to forests

318 worldwide (Bennett et al., 2015), was driven primarily by their height (Stovall et al., 2019). We found only a

319 marginal additional effect of crown exposure, with a tendency for lowest Rt among the most exposed

320 (dominant) and suppressed trees. The negative effect of height on Rt held after accounting for species' traits.

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There was no evidence that soil water availability increased drought resistance; in contrast, trees in wetter topographic positions had lower Rt (Zuleta et al., 2017; Stovall et al., 2019), and the larger potential rooting volume of large trees provided no advantage in the drier microenvironments. Drought resistance was not linked to species' LMA, wood density, or xylem type (ring- vs. diffuse porous), but was negatively correlated with leaf hydraulic traits (PLA_{dry}, π_{tlp}). This is the first report to our knowledge linking PLA_{dry} and π_{tlp} to growth reduction during drought. The directions of these responses were consistent across droughts, supporting the premise that they were driven by fundamental physiological mechanisms. However, the strengths of each predictor varied across droughts (Fig. 4; Tables S6-S7), indicating that drought characteristics interact with tree size, microenvironment, and traits to shape which individuals are most affected. These findings advance our knowledge of the factors that make trees vulnerable to growth declines during drought–and, by extension, likely make them more vulnerable to mortality (Sapes et al., 2019).

The droughts considered here were of a magnitude that has occurred with an average frequency of approximately once every 10-15 years (Fig. **1a**, Helcoski et al. (2019)) and had substantial but not devastating impacts on tree growth (Figs. **1b, 2**). These droughts were classified as severe (1977) or extreme (1966, 1999) according to the PDSI metric and have been linked to tree mortality in the eastern United States (Druckenbrod et al., 2019); however, extreme, multiannual droughts or so-called "megadroughts" of the type that have triggered massive tree die-off in other regions (e.g., Allen et al. (2010); Stovall et al. (2019)) have not occurred in the Eastern United States within the past several decades (Clark et al., 2016). Of the droughts considered here, the 1966 drought, which was preceded by two years of dry conditions (Fig. **S2**), severely stressed a larger portion of trees (Fig. **1b**). The tendency for large trees to have lowest resistance was most pronounced in this drought, consistent with other findings that this physiological response increases with drought severity (Bennett et al., 2015; Stovall et al., 2019). Across all three droughts, the majority of trees experienced reduced growth, but a substantial portion had increased growth (Fig. **1b**), potentially due to decreased leaf area of competitors during the drought (**REF–if we can find one**), and consistent with prior observations that smaller trees can exhibit increased growth rates during drought (Bennett et al., 2015). It is likely because of the moderate impact of these droughts, along with other factors influencing tree growth (e.g., stand dynamics), that our best models characterize only a modest amount of variation in Rt: 11-12% for all droughts combined, and 18-26% for each individual drought (Table S6).

Our analysis indicates that tree height has a stronger influence on drought response than does canopy position (Fig. 4; Tables 1, S6-S7). This is consistent with, and reinforces, previous findings that biophysical constraints make it impossible for trees to efficiently transport water to great heights and simultaneously maintain strong resistance and resilience to drought-induced embolism (Olson et al., 2018; Couvreur et al., 2018; Roskilly et al., 2019). However, the collinearity between the two variables (Fig. **3d**) makes it impossible to confidently partition causality. Taller trees are more likely to be in dominant canopy positions (Fig. **3d**) and, largely as a consequence of their position relative to others, face different microenvironments (Fig. **3a-b**). Even under non-drought conditions, evaporative demand and maximum leaf temperatures increase with tree height (Smith and Nobel, 1977; Bretfeld et al., 2018; Kunert et al., 2017), and such conditions would incur additional stress during drought, when solar radiation tends to be higher and less water is available for evaporative cooling of the leaves (*Campbell & Norman REF*). However, some decoupling between height and canopy position is introduced by the configuration of neighboring trees (Fig. **3d**) (Muller-Landau et al., 2006), and height was an overall stronger predictor of drought response than crown position (Fig. 4; Tables 1, S6-S7). Belowground, taller trees would tend to have larger root systems,

but the potentially greater access to water did not override the disadvantage conferred by height–and, in fact, greater moisture access in non-drought years (here, higher TWI) appears to make trees more sensitive to drought (Zuleta et al., 2017; Stovall et al., 2019).

Our analysis has the limitation that canopy positions were recorded in 2018, as opposed to the years of the droughts. However, because trees would generally advance towards more dominant positions as they grow and as neighbors die, changing canopy positions would bias against the acceptance of our hypothesis. The implication is that dominant crown positions did have a marginally negative influence on Rt, which makes sense in light of the vertical environmental gradients described above and agrees with previous studies showing lower drought resistance in more exposed trees (Liu and Muller, 1993; Suarez et al., 2004; Scharnweber et al., 2019). It is safe to assume that currently suppressed trees were suppressed throughout our analysis period, and their relatively low Rt (after accounting for height effects) is real, perhaps as a result of competition (Sohn et al., 2016). The observed height-sensitivity of Rt, together with the lack of advantage to large stature in drier topographic positions, agrees with the concept that physiological limitations to transpiration under drought shift from soil water availability to the plant-atmosphere interface as forests age (Bretfeld et al., 2018), such that tall, dominant trees are the most sensitive in mature forests. Additional research comparing drought responses of young and old forest stands, along with short and tall isolated trees, would be valuable for more clearly disentangling the roles of tree height and crown exposure.

The development of tree-ring chronologies for the twelve most dominant tree species at our site (Helcoski et al., 2019; Bourg et al., 2013) gave us the sample size to compare historical drought responses across species (Fig. **2**) and associated traits at a single site (see also Elliott et al., 2015). Concerted measurement of leaf hydraulic traits of emerging importance (Scoffoni et al., 2014; Bartlett et al., 2016; Medeiros et al., 2019) allowed novel insights into the role of hydraulic traits in shaping drought response. The finding that PLA_{dry} and π_{tlp} can be useful for predicting drought responses of tree growth (Tables 1,4,5) is both novel and consistent with previous studies linking these traits to habitat and drought tolerance. Previous studies have demonstrated that π_{tlp} and PLA_{dry} are physiologically meaningful traits linked to species distribution along moisture gradients (Maréchaux et al., 2015; Fletcher et al., 2018; Medeiros et al., 2019; Simeone et al., 2019; Rosas et al., 2019), and our findings indicate that these traits also influence drought responses. Furthermore, the observed linkage of π_{tlp} to Rt in this forest aligns with observations in the Amazon that π_{tlp} is higher in drought-intolerant than drought-tolerant plant functional types and adds support to the idea that this trait is useful for categorizing and representing species' drought responses in models (Powell et al., 2017). Because both PLA_{dry} and π_{tlp} can be measured relatively easily (Bartlett et al., 2012; Scoffoni et al., 2014), they hold promise for predicting drought growth responses across diverse forests. The importance of predicting drought responses from species traits increases with tree species diversity; whereas it is feasible to study drought responses for all dominant species in most boreal and temperate forests (e.g., this study), this becomes difficult to impossible for species that do not form annual rings, and for diverse tropical forests. Although progress is being made for the tropics (Schöngart et al., 2017), a full linkage of hydraulic traits to drought responses would be invaluable for forecasting how little-known species and whole forests will respond to future droughts (Powell et al., 2017).

As climate change drives increasing drought in many of the world's forests (Trenberth et al., 2014; Intergovernmental Panel on Climate Change, 2015), the fate of forests and their climate feedbacks will be shaped by the biophysical and physiological drivers observed here. Large trees have been disproportionately impacted by strong drought in forests around the world (Bennett et al., 2015; Stovall et al., 2019), and we

show, at least at this site, that this is primarily driven by their height, potentially with some contributions from canopy position. The distinction is important because it suggests that height *per se* makes trees vulnerable, even if their crowns are somewhat protected by neighbors, whereas shorter solitary trees or the dominant trees in young forests that recently established after logging or natural disturbances should be less vulnerable. This would suggest that, all else being equal, mature forests would be more vulnerable to drought than young forests with short trees; however, root water access may limit the young forests (Bretfeld et al., 2018), and species traits often shift as forests age. Early- to mid- successional species at our site (*Liriodendron tulipifera*, *Quercus spp.*, *Fraxinus americana*) display a mix of traits conferring drought tolerance and resistance (Table 3), and further research on how hydraulic traits and drought vulnerability change over the course of succession would be valuable for addressing how drought tolerance changes as forests age (e.g. Rodríguez-Catón et al., 2015). In the meantime, the results of this study advance our knowledge of the factors conferring drought resistance in a mature forest, opening the door for more accurate forecasting of forest responses to future drought.

Acknowledgements

Author Contribution

KAT, IM, and AJT designed the research. Tree-ring chronologies were developed by RH under guidance of AJT and NP. Trait data was collected by IM, JZ under guidance of NK and LS. Other plot data were collected by IM, AS, EGA, and NB under guidance of EGA and WM. Data analyses were performed by IM under guidance of KAT and VH. KAT and IM interpreted the results. IM and KAT wrote the first draft of manuscript, and all authors contributed to revisions.

Supplementary Information

Table S1: Species-specific bark thickness regression equations

Table S2: Species-specific height regression equations

Table S3: Palmer drought severity index (PDSI) by month for focal droughts

Figure S1: Map of ForestGEO plot showing TWI and location of cored trees

Figure S2: Time series of Palmer Drought Severity Index (PDSI) for the 2.5 years prior to each focal drought

Figure S3: Height (from reconstructed DBH) by canopy position across the three focal droughts and in the year of measurement (2018)

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